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Vicia menziesii Sprengel (Fabaceae) Rediscovered: Its Taxonomic Relationships[1]

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ABSTRACT: Taxonomic relationships among five taxa of *Vicia*, traditionally recognized at the species level, were studied. Data used included plant and seed morphology, seed amino acid content, palynology, and cytology. Two Old World species, *V. dumetorum* Linnaeus and *V. pisiformis* Linnaeus, are shown not to be closely related to the Hawaiian and American taxa. The Hawaiian species, *V. menziesii* Sprengel, is maintained as a species and is shown to be closely related to *V. gigantea* Hooker of North America and *V. nigricans* Hooker & Arnott of South America. The latter two species are treated as subspecies under the name *V. nigricans*. The karyotype and chromosome number are reported for the first time for the endangered species, *V. menziesii*.

Vicia menziesii Sprengel, which is endemic to the island of Hawaii and was last collected in 1915, has been regarded as extinct. It was rediscovered in 1973 on the same island by Wayne Gagné and Mae Mull (C. H. Lamoureux and D. Herbst, personal communications). It is now considered an endangered species (United States Department of the Interior 1978). This species was not mentioned by Kupicha (1976) when she presented a general worldwide taxonomic treatment of the genus.

Vicia menziesii exhibits these diagnostic characters: (1) plants large, rank and darkening or blackening with age or on drying; (2) mature flowers rose-purple; (3) oblong standard; (4) compressed styles with encircling apical hairs; (5) stipitate legumes without inner "woolly" parenchymatous tissue; (6) seeds with hilum occupying 75 percent of the seed circumference and containing canavanine; (7) six pairs of acrocentric chromosomes, one pair with satellites, and one submetacentric pair; and (8) seedlings with the first eophylls at the fourth node and the first three eophylls each bearing four leaflets and a tendril.

A review of New and Old World vetches located four other species with diagnostic characters similar to those of *Vicia menziesii*: *V. nigricans*, *V. gigantea*, *V. pisiformis*, and *V. dumetorum*. Although Kupicha (1976) apparently combines *V. nigricans* Hooker & Arnott of Chile and Argentina and *V. gigantea* Hooker of the Pacific Northwest of North America, she neither formally proposed this combination nor made any taxonomic judgment at the subspecific level. These three New World taxa were originally described as species: *V. menziesii* in 1826, *V. nigricans* in 1830, and *V. gigantea* in 1831. They traditionally have been treated as species in various floras or monographs of their respective geographical regions (Degener, Degener, and Gunn 1970, Hermann 1960, Reiche 1898, Welsh 1974). *Vicia pisiformis* Linnaeus of middle Europe and *V. dumetorum* Linnaeus of Eurasia have been treated as species in various floras or monographs of their respective geographical regions (Ball 1968, Fedtschenko 1948), and both were studied by Kupicha.

MATERIALS AND METHODS

Specimens from the following herbaria were examined: BAFC, BISH, CONC, F,

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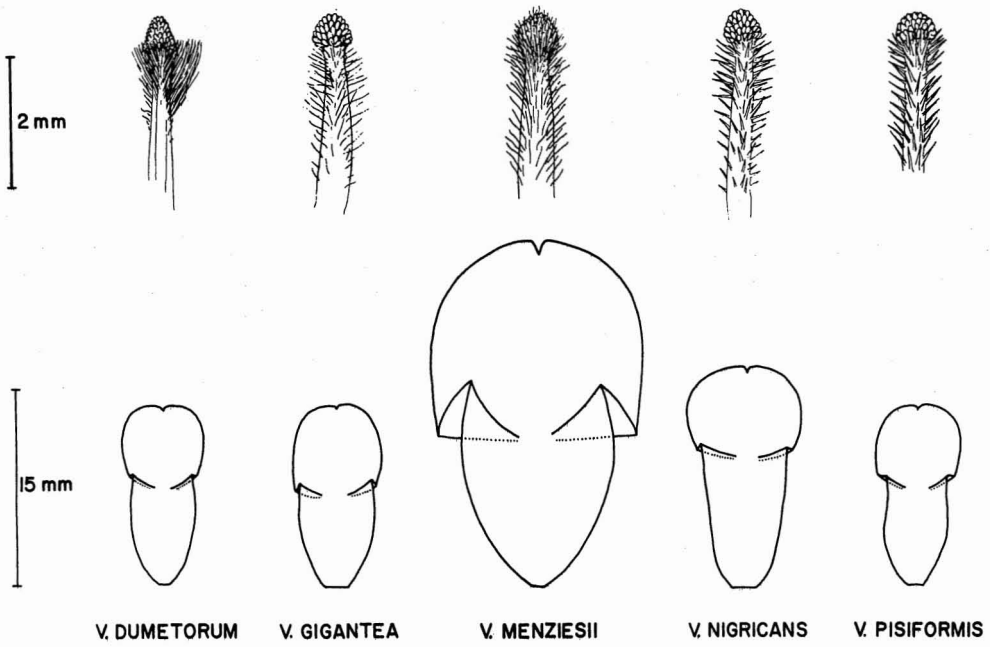

FIGURE 1. Styles (top row) and standards (bottom row) of five species of *Vicia*.

GH, NA, NY, R, SGO, SP, US [herbarium abbreviations throughout this paper defined by Holmgren and Keuken (1974)]. Morphological characters examined include those used by Gunn (1968), Lassetter (1975, 1978), and Kupicha (1976). External seed characters were compared, and seed amino acid contents were evaluated. Pollen was examined, and karyotypes were compared. No artificial hybridizations of these perennials could be attempted due to lack of suitable growth chambers that would provide cool temperatures and high humidity required by the taxa. Greenhouse and field plot attempts to grow *Vicia gigantea* and *V. nigricans* at Beltsville, Maryland, failed to produce flowering plants. No attempt was made to grow *V. menziesii* to flower.

RESULTS AND DISCUSSION

Vicia menziesii, *V. nigricans*, and *V. gigantea*, but not *V. pisiformis* and *V. dumetorum*, usually darken or blacken with age or upon drying due to the presence of L-3, 4-dihydroxyphenylalanine (L-dopa) (Andrews and Pridham 1967). When lengths of flowers, leaflets, legumes, seeds, hila, or stems are considered, these five species are among the largest in the genus.

Vicia nigricans and *V. gigantea* have ochreoleucous to orange flowers, often with a tinge of rose-purple. *Vicia menziesii* flowers are ochreoleucous when young and rose-purple when mature. *Vicia dumetorum* is blue-purplish flowered, and *V. pisiformis* is yellow flowered. Although the significance of flower color may not have been adequately surveyed for the genus, Kupicha (1976) noted that it is of little value at the section level. Among the native North American species, *V. gigantea* is the only species with ochreoleucous to orange flowers tinged with rose-purple. If Hawaii is considered, *V. menziesii* is the only native New World–Oceania species with a distinct rose-purple pigment in the flower. The rose-purplish pigment in both species becomes more pronounced as flowers age. Burkart (1966), Moore and Scotter (1976), and Reiche (1898) listed about 33 native species for South America. About 20 of the 33 species are valid and only 7 of these have ochreoleucous

to orange or reddish flowers. Four of these represent forms of *V. nigricans* and should be regarded as synonyms. Flowers of the other native North and South American species are bluish, white, lavender, or purple, but never with a definite orangy or rose-purple color.

The shape of the standard in all five species is oblong (Kupicha 1976 and Figure 1).

The nature of stylar pubescence and compression of the style is an important morphological character in *Vicia* (Gunn and Kluve 1976, Kupicha 1976, Lassetter 1975). Gunn and Kluve found that about 40 percent of the 106 species surveyed had apical hairs encircling the style. Members of several of Kupicha's sections, including Cassubicae with *V. nigricans* and Vicilla with *V. pisiformis* and *V. dumetorum*, have stylar pubescence distributed evenly around the style. *Vicia dumetorum* is an exception in its section, because its stylar pubescence is densely concentrated on the abaxial side (Figure 1). The other four species in this study have evenly pubescent styles, the predominant condition in the subgenus *Vicilla*. Compression of styles is dorsal in all five species. Kupicha discussed the types of stylar compression.

The legumes of the five species are similar, except that those of *Vicia menziesii* may be much larger. These general legume characters are typical for the subgenus *Vicilla* (Kupicha 1976).

All five species have a circumlinear hilum that occupies 75 percent of the seed circumference. Only 15 percent of 100 species (± 150 species in the genus) surveyed exhibited a circumlinear hilum (Gunn 1970). The seeds of the five species have a similar external morphology, except that *Vicia menziesii* seeds average about 25 percent greater in diameter (Figure 2).

On the basis of seed amino acid data, Bell (1971) divided *Vicia* into three groups: (1) canavanine-producing species; (2) species not producing canavanine but having high concentrations of γ-glutamyl-β-cyanoalanine and lower concentrations of free β-cyanoalanine; and (3) species without canavanine and without compounds in the second group. In a similar study, Tschiersch and Hanelt (1967) also established three groups: (1) canavanine-producing species; (2) species without canavanine but with β-cyanoalanine and its γ-glutamyl derivative; and (3) species without canavanine but with high levels of arginine. Tschiersch and Hanelt (1967) placed *V. dumetorum* and *V. pisiformis* in their group 3. Of the five species under consideration, only *V. dumetorum* was included by Bell and Tirimanna (1965) and Bell (1966) when they surveyed the genus for seed amino acid content. This species contains γ-hydroxyarginine and an additional compound which is probably hydroxycitrulline (Bell 1966; Bell, personal communication). *Vicia pisiformis*, analyzed at a later time, exhibited no amino acid pattern typical for the genus. It contains an unusual neutral amino acid and an unusual acidic amino acid (Bell, personal communication). Based on this biochemical comparison, *V. dumetorum* and *V. pisiformis* are different. Tschiersch and Hanelt (1967) found that *V. dumetorum* and *V. pisiformis* were similar, differing only in amounts of threonine and arginine and in presence or absence of alanine. These authors, however, may not have analyzed for the neutral and acidic acids Bell found in *V. pisiformis*. Their data show that neither species is a canavanine producer. *Vicia menziesii*, *V. nigricans*, and *V. gigantea* contain appreciable amounts of canavanine with no trace of β-cyanoalanine or γ-glutamyl-β-cyanoalanine (Bell and B. V. Charlwood, personal communications). This would place these vetches in the canavanine-containing group of Bell and Tschiersch and Hanelt. Tschiersch and Hanelt (1967) stated that biochemically defined species groupings and taxonomically (they presumably mean morphological data) defined groups are never completely identical. Bell (1971) similarly noted that his three main groups correspond in general to accepted subgeneric groups based on morphology and cytology. These groups predate Kupicha's report, and in this instance the biochemical and morphological data mesh. Kupicha (1976) placed *V. pisiformis* and *V. dumetorum* in a different section from *V. nigricans*.

It has been clearly established that karyo-

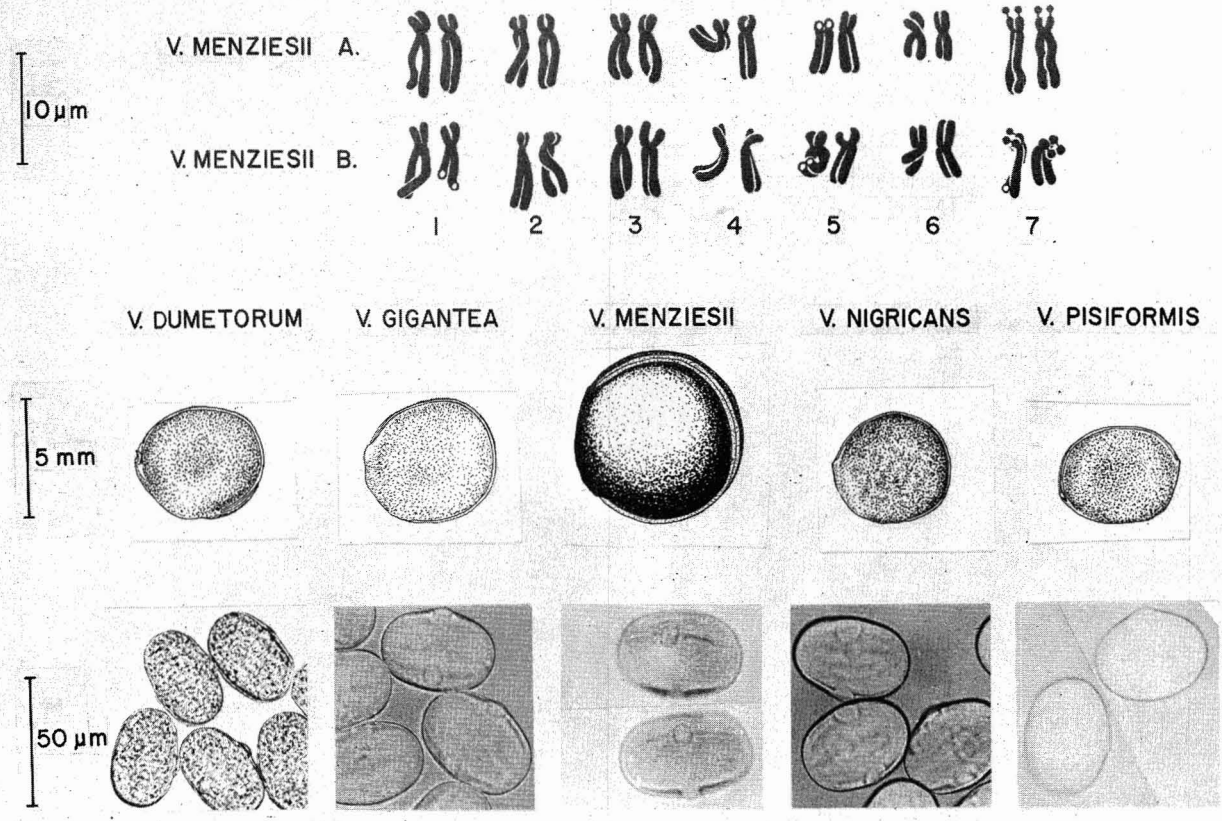

FIGURE 2. Idiograms of *Vicia menziesii* Sprengel (top row) and seeds (middle row) and pollen (bottom row) of five species of *Vicia*.

typic differences are taxonomically significant at the species level (Kupicha 1976, Lassetter 1975, Mettin and Hanelt 1968, Shrivastava 1963, Stankevich 1970, Sveshnikova 1927). The karyotype of *Vicia pisiformis* was reported by Činčura (1962) and the karyotype of *V. dumetorum* by Terziiski (1974) Činčura (1973) presented a morphological and cytological comparison of the two species. Terziiski and Činčura confirmed the earlier work of Heitz (1931), who presented chromosome numbers and karyotypes of both species. According to them, *V. dumetorum* is $2n = 14$, *V. pisiformis* is $2n = 12$, and each contains one satellited pair. Činčura (1973) determined that five chromosome pairs are essentially the same in size and characteristics in both species. These include one metacentric pair, two submetacentric pairs, and two acrocentric pairs (one of these is the satellited pair). There is a difference in the longest pair: In *V. pisiformis* it is longer and more nearly metacentric. The third pair in *V. dumetorum* (which is submetacentric and equals pair *F* according to Terziiski) is not present in *V. pisiformis*. Činčura (1973) concluded that these vetches are closely related species, occupying similar habitats, but that they are morphologically and karyologically definable and separable from one another. *Vicia menziesii* has $2n = 14$ chromosomes with one satellited pair (Figure 2). Pair 6 is submetacentric and all others are acrocentric. The karyotypes of *V. gigantea* and *V. nigricans* are identical to each other (S. Veerasethakul, unpublished data) but different from *V. menziesii*. In the former two species, the satellited pair of chromosomes is smaller and pair 6 is acrocentric, whereas pair 6 in *V. menziesii* is submetacentric and the satellited pair is much larger. Also, a minor difference exists in pair 5: In *V. menziesii*, pair 5 is less strongly acrocentric, and in the other two species it is more so. The other chromosome pairs, 1–4, are comparable in size and characteristics and are believed to be essentially the same. *Vicia menziesii* voucher A was deposited in the Eastern Kentucky University Herbarium and voucher B in ISC.

Nozzolillo (1977) presented a study of *Vicia* seedlings. She was aware of our concurrent work on the taxonomic relationship of *V. nigricans* and *V. gigantea* and treated them as a single species, but she had no *V. menziesii* seedlings. Observations from our chromosome vouchers show that eophylls of *V. menziesii* first appeared at the fourth node and that the first three eophylls on both plants each had four leaflets and a tendril. These characteristics place *V. menziesii* very close to *V. nigricans* in Nozzolillo's key. Because the leaflets are only two to three times as long as wide, *V. menziesii* would be placed with *V. sylvatica*, a species of section Vicilla according to Kupicha (1976). The wide leaflets of *V. menziesii* are typical of its gigantism (see discussion under *Vicia menziesii*.) In general, *V. menziesii* seedlings are similar to those of *V. nigricans*. *Vicia pisiformis* and *V. dumetorum* are alike according to Nozzolillo, but are in a different group of species that have only two leaflets in the first three eophylls.

A cursory study of *Vicia* pollen as part of a larger tribal survey (Clarke and Kupicha 1976) did not reveal major intrageneric variation (Kupicha 1977). The pollen is oblong, with small, heavily thickened endoapertures. Pollen of all five species in this study is similar (Figure 2) and resembles pollen grains of the *V. ludoviciana* complex (Lassetter 1972). Erdtman (1952) concluded that there are no striking differences among the pollen of the three subfamilies of Fabaceae.

TAXONOMIC TREATMENT

Vicia menziesii is closely related to the New World continental species *V. gigantea* and *V. nigricans*. Its isolated and endemic range, coupled with its physical size, karyotype differences, larger rose-purple flowers, lack of pellucid dots on leaflets, and possible pollinators (see following discussion) make it a valid species. The continental taxa, because of identical karyotypes, habitats, and other similarities, should best be viewed as disjunct subspecies. These two taxa are combined under the earlier of the two names,

FIGURE 3. Illustration of *Vicia menziesii* Sprengel.

Vicia nigricans Hooker & Arnott. Based on data presented in this paper, *V. dumetorum* and *V. pisiformis*, a related species-pair, are not closely related to the other three taxa.

In the following discussion, an exclamation mark indicates that the type specimen or its photograph was examined. The abbreviation F.M. Neg. indicates the negative number of the Field Museum's series of negatives taken in European herbaria by J. F. Macbride from 1929 to 1939.

Vicia menziesii Sprengel, Car. Linn. Syst. Veget. ed. 16, 3:267. 1826.

Figure 3

HOLOTYPE: "At the upper edge of the forest on the mountain Mowna-rooa, in Owhyee which is 6,000 feet high," A. Menzies 1803 (LINN!).

ISOTYPE (BM!): *Vicia grandiflora* Smith in Rees, Cyclop. 37, no. 7. 1819; non *V. grandiflora* Scopoli, Fl. Carn. ed. 2, 2:65. 1772.

DESCRIPTION: Coarse, strongly climbing, perennial herb 15-90-(200) dm long; pubescent when young, less so at maturity, darkening with age or on drying; stems stout, 6 to 8 mm thick, fistulose, conspicuously ridged; stipules large, 20 to 30 mm long, 10 to 20 mm wide, foliaceous, suborbicular, lacerate–dentate with long subulate teeth; leaves 10 to 13 cm long, ending in ramose tendril; leaflets alternate or subopposite, 8 to 12, entire, ovate lanceolate to ovate, 35 to 70 mm long, 15 to 30 mm wide, acute to rounded at mucronulate apex, pubescent when young, with few scattered fine hairs with age, neither side bearing pellucid dots; flowering peduncles slightly shorter than the subtending leaves, lengthening during fruiting, with six to nine loosely clustered racemose flowers, pedicels 8 to 10 mm long; corolla quite large, 25 to 30 mm long, sharply curved, ochre-oleucous when young and becoming rose-purple with age; calyx gibbous, tube less than one-half length of corolla, upper pair of teeth 3 to 5 mm long, lateral pair 5 to 6 mm, lowest tooth 6 to 7 mm and subequal to tube; androecial sheath oblique at apex; pollen tricolporate, prolate, 50 × 32 micra; style dorsally flattened, the upper portion encircled by delicate hairs; legume glabrous, oblong, 90 to 100 mm long, 15 to 20 mm wide, becoming black at maturity, smooth within, with more than four ovules, on 10-mm stipe; seed spherical, smooth, monochrome blackish, 6 to 8 mm in diameter, containing canavanine; hilum color of seed coat, circumlinear, occupying 75 percent of the seed circumference.

FLOWERING: June. Chromosome number: $2n = 14$, Hawaii Island, 15 km northwest of Volcano, Keauhou Ranch, 1700 m. Seeds collected by C. J. Ralph and H. Sakai.

DISCUSSION: This species was first named *Vicia grandiflora* by Smith. The holotype is in the Smith Herbarium at LINN. However, Smith's *V. grandiflora* is an illegitimate homonym. Sprengel later proposed the name *V. menziesii* in honor of the original collector, A. Menzies. The Federal Register (United States Department of the Interior 1978) promulgated the poorly coined common name "Hawaiian wild broad-bean." The term *broad-bean* is generally restricted to one species of *Vicia*, *V. faba*. A far better common name is "Hawaiian vetch."

Vicia menziesii is the only vetch native in Oceania (Figure 4). Its original range was apparently restricted to forest slopes of Mauna Loa and possibly Mauna Kea at about 2000 to 2500 m, as determined by Skottsberg (1931), although he did not personally see living specimens. Hillebrand (1888) also stated that it occurred on Mauna Kea, but we have not personally seen a Mauna Kea collection. Until 1973, when it was rediscovered by Wayne Gagné and Mae Mull (C. H. Lamoureux and D. Herbst, personal communications), the last known collection was by Forbes in 1915 (Rock 1920).

Since this initial rediscovery, five colonies with 15 plants have been located in the same general area. The major colony is 15 km northwest of Volcano on private land at 1500 to 1700 m elevation (C. J. Ralph, personal communication). Quick action was taken by interested people in Hawaii, and the species is now protected as an endangered

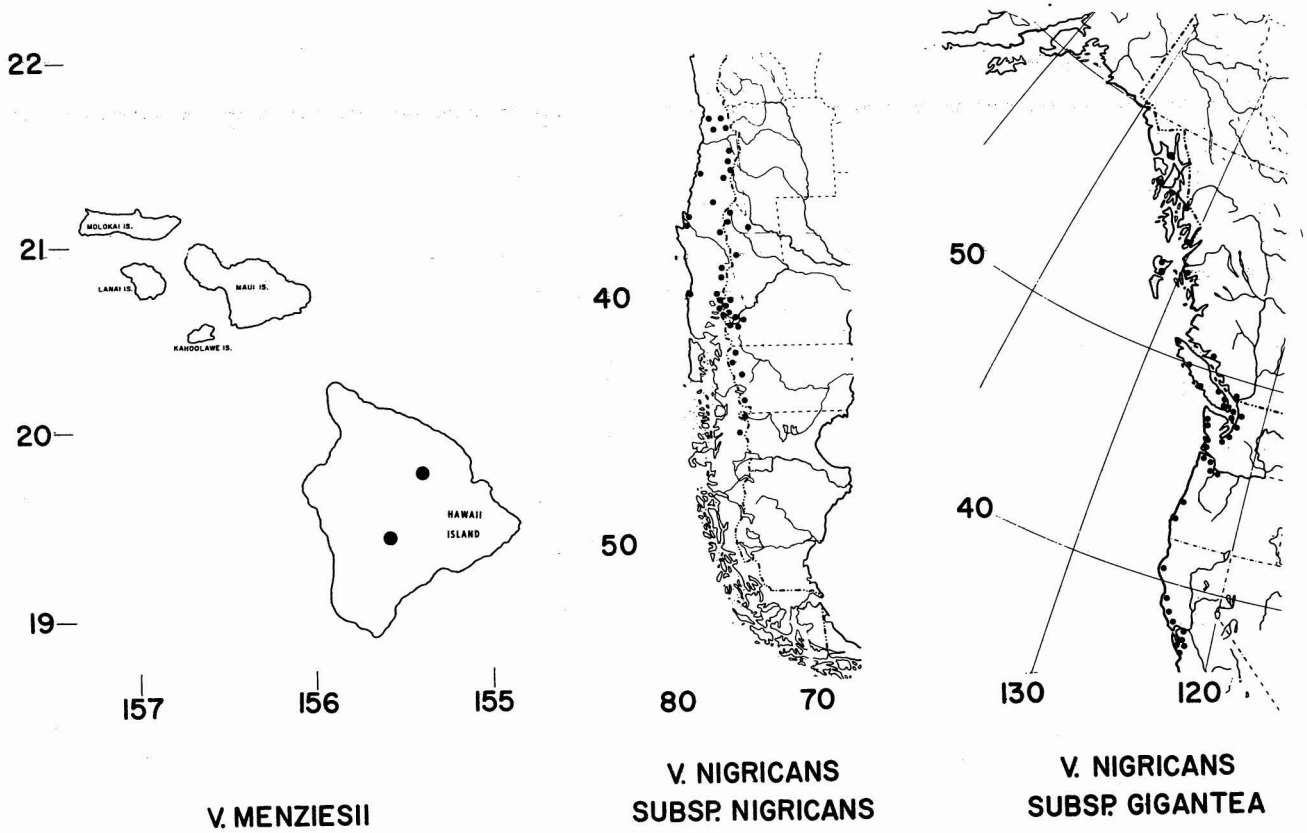

FIGURE 4. Distribution of *Vicia menziesii* Sprengel, *V. nigricans* Hooker & Arnott subsp. *nigricans*, and *V. nigricans* Hooker & Arnott subsp. *gigantea* (Hooker) Lassetter & Gunn.

species (Fosberg and Herbst 1975, United States Department of the Interior 1978).

According to C. J. Ralph (personal communication), the main stem of *Vicia menziesii* may grow upward into the subcanopy of *Metrosideros collina* ssp. *polymorpha* and then often branches laterally. Stems up to 20 m in length have been observed. An individual plant can contain as many as 20 flower clusters and about 90 flowers.

Examples of gigantism are common among oceanic island species. In Hawaii, several legumes as well as other plants show a trend toward larger fruits and/or seeds from smaller, presumably more transportable ancestral forms. Larger seeds are believed better for competing and surviving on the terrestrial areas of the islands (Carlquist 1974). *Vicia menziesii* has the largest seeds of the three taxa, and indeed, has the ninth largest seed of the 100 species included by Gunn (1970). No extensive listing of legume size for the genus was found, but a comparison with species included in Gunn (1971) and Hermann (1960) showed that *V. menziesii* has larger legumes than all vetches listed except *V. faba*, *V. narbonensis*, and *V. sativa* (all human-influenced species). Leaflets are also among the largest in the genus.

Carlquist (1974) stated that most flowers of oceanic island species are small, with red being the least frequent color. These characters were related to small insects available to perform pollination. *Vicia menziesii*, however, has large flowers that turn rose-purple on maturation, an exception to the general correlation of Carlquist.

C. J. Ralph (personal communication) reported that two species of native birds feed at *Vicia menziesii* and possibly pollinate it. The 'I'iwi (*Vestiara coccinea*) has a down-curved bill that fits the curve of the corolla, and the birds turn the flowers upside down to feed. 'Amakihi (*Loxops virens*) has a similar but smaller bill, and somewhat damages flowers when it feeds. This bird–flower relationship may explain why mature flowers are large and rose-purple.

SPECIMENS: Apparently very few specimens of *Vicia menziesii* exist. We have listed all of which we are aware. Hawaii Island: C. N. Forbes 938-H (BISH, NY, two duplicates of this collection are at BM but were not seen); M. J. Remy 656 (GH, this sheet is ex P, duplicates may exist there); F. R. Warshauer & G. Murakami 1240 (US); A. Menzies (BM photograph). Rock (1920) states that Macrae also collected *V. menziesii*; we have not seen these specimens, but judging from Mann (1866), specimens might be at CGE, G, or K. Approximately the same number of specimens we examined was used in the treatment of this species by Degener et al. (1970).

Vicia nigricans Hooker & Arnott subsp. *nigricans*

Figure 5

Vicia nigricans Hooker & Arnott, Bot. Capt. Beechey's Voy. 20. 1830
Ervum nigricans (Hooker & Arnott) Alefeld in Oesterr. Bot. Zeit. 9(11):364. 1859

HOLOTYPE: Concepción, Chile. Beechey (K!). *Lathyrus macraei* Hooker & Arnott, Bot. Capt. Beechey's Voy. 21. 1830. *V. macraei* Hooker & Arnott, Bot. Misc. 3:195. 1833 (HOLOTYPE K!). *V. magnifolia* Clos in Gay, Fl. Chile 2:135. 1847. *V. macraei* var. *valdiviana* Philippi, Linnaea 33:51. 1864–1865. *V. lanceolate* Philippi 1.c.51. *V. leyboldii* Philippi 1.c.51 (HOLOTYPE: SGO!, ISOTYPE: F.M. Neg. 2341 ex B!). *V. andina* Philippi, Anal. Univ. Chile 41:692. 1872 (HOLOTYPE: SGO!, ISOTYPE: F.M. Neg. 2336 ex B!). *V. fodinarum* Philippi 1.c.692. *V. moorei* Philippi, Anal. Univ. Chile 84:270. 1894 (HOLOTYPE: SGO!). *V. apiculata* Philippi 1.c.274 (HOLOTYPE: SGO!). *V. coxii* Philippi 1.c.275 (HOLOTYPE: SGO!). *V. commutata* Philippi 1.c.276 (HOLOTYPE: SGO!). *V. darapskyana* Philippi 1.c.276 (HOLOTYPE: SGO!). *V. speciosa* Philippi 1.c.277 (HOLOTYPE: SGO!). F.M. Neg. 2334 ex B! is of a Poeppig specimen, the name for which has not been validly published.

DESCRIPTION: Coarse, strongly climbing perennial herb 20 to 30 dm tall; pubescent

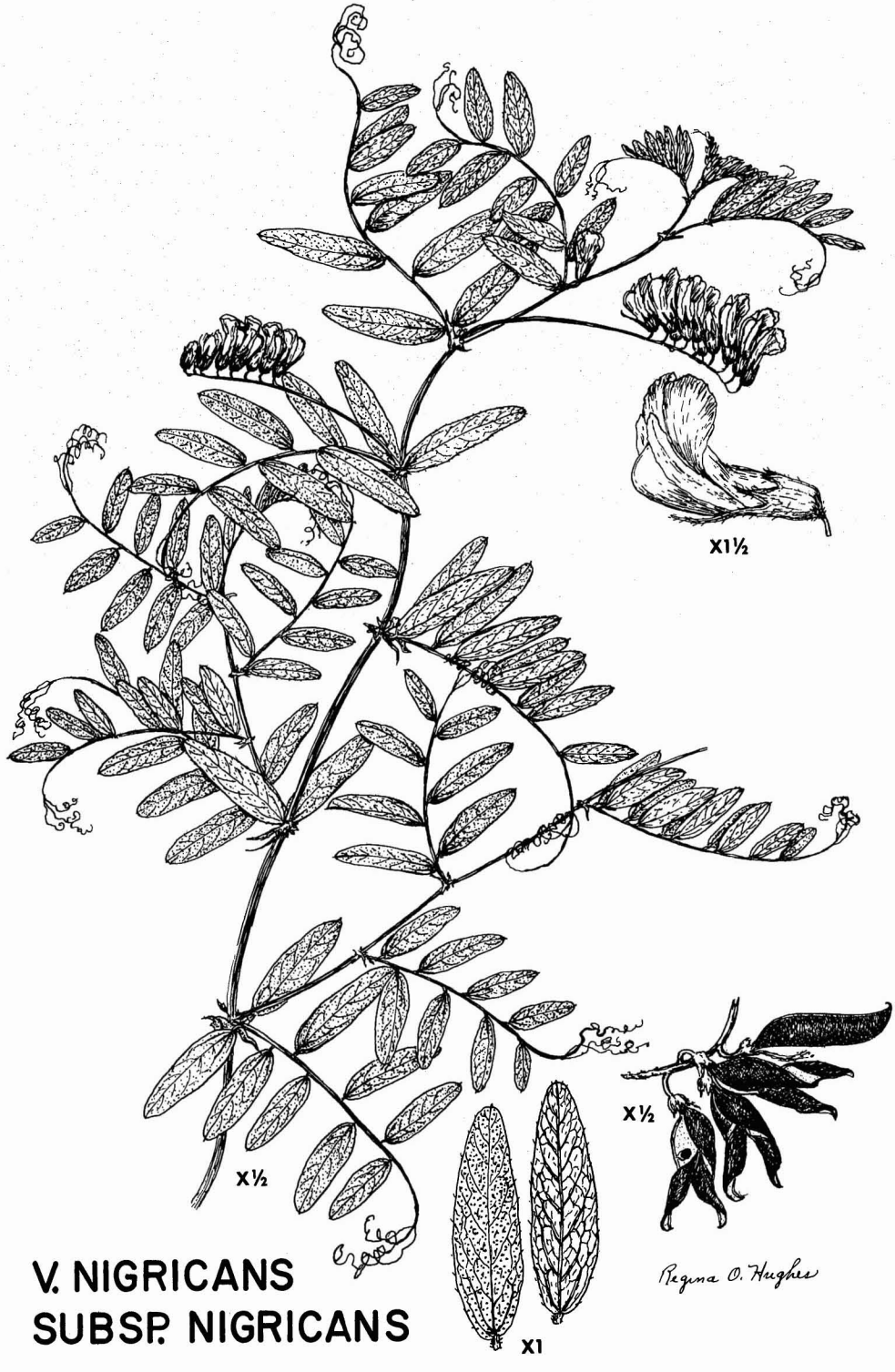

FIGURE 5. Illustration of *Vicia nigricans* Hooker & Arnott subsp. *nigricans*.

when young, becoming less so at maturity, turning black with age or on drying, sometimes remaining green; stems stout, 1 to 7 mm thick, fistulose, usually conspicuously ridged; stipules moderately large (up to 14 mm long and 7 mm wide), semisagittate, or occasionally orbicular and foliaceous, but upper portion usually not foliaceous, lower portion entire or deeply angled and with two to three teeth; leaves 5 to 23 cm long, ending in a ramose tendril; leaflets alternate or subopposite, 6-14-(18), entire, linear–lanceolate, lanceolate to ovate and widely elliptic, 11 to 50 mm long, 5 to 20 mm wide, acute, obtuse, rounded, or truncate to emarginate at the mucronulate apex, pubescent when young, mature leaflets usually somewhat strigose and obscurely pellucid dotted below, usually glabrous with prominent pellucid dots above; flowering peduncles averaging slightly longer than subtending leaves but often shorter or up to twice the leaf length, lengthening during fruiting, with 4 to 25 closely packed racemose flowers; pedicels 1.5 to 7 mm long; corolla 13 to 24 mm long, ochreoleucous to orange, often tinged with rose-purple; calyx gibbous, tube about one-fourth to one-third length of corolla, upper pair of teeth 0.3 to 1.4 mm long, lateral pair 0.4 to 5 mm long, lowest tooth 1.3 to 6.2 mm long, much shorter to slightly longer than tube, averaging about three-fourths length of tube; androecial sheath oblique at apex; pollen tricolporate, prolate, 45 × 32 micra; style dorsally flattened, upper portion encircled by rather stout hairs; legume glabrous, oblong, 37 to 46 mm long, 8 to 10 mm wide, becoming black at maturity, smooth within, four to nine ovuled, on a (1.5)-4-6 mm stipe; seed usually three to four per legume, spherical, smooth, monochrome reddish-ochre to darker brown, 5 to 6 mm in diameter, containing canavanine; hilum color of seed coat, circumlinear, occupying 75 percent of the seed circumference.

FLOWERING: October through March. Chromosome number: $n = 7$, Quebrada Macul, Santiago, Chile (Cortazar 1948). The voucher specimen is *Vicia macraei* Pisano 1577, 1948 (SGO!). Cortazar stated that the observations were made on sexual cells, but the drawing is clearly of mitotic chromosomes. $2n = 14$, S. Veerasethakul (unpublished data).

DISCUSSION: Hooker and Arnott described *Vicia nigricans* in 1830 and *V. macraei* in 1833 when the two were compared. Only minor differences between the two species were listed. All vegetative characteristics they mentioned are now known to intergrade, and we believe that such variation is best viewed as expected phenotypic plasticity not warranting a species-level distinction. The holotype of *V. macraei* (6 to 9 leaflets from the description) has several leaves with 15 leaflets and one with 17. Hooker and Arnott also stated that *V. macraei* discolors but does not blacken; this characteristic also is variable. *Vicia faba*, which is not related to these taxa, also often turns blackish upon drying, but not every individual does so, and the degree of darkening varies. Likewise, Philippi at various times (see synonomy citations) named many phenotypic variants as species. An example is his *V. fordinarum*, which is distinguished from *V. macraei* by its large stipular teeth.

Vicia nigricans subsp. *nigricans*, the largest known South American vetch, is restricted to the mountains of central Chile from Valparaiso Provincia to Aysen Provincia and to the mountains of extreme western Argentina in the National Territories of Neuquen, Rio Negro, and Chubut (Figure 4). This taxon follows the distribution of the austral *Nothofagus* forest and is usually found associated with it. Masses of plants may be found in open to semiopen areas within the forest or along the edges of the granite slopes of the Andes from 850 to 1250 m.

Judging from the material of *V. nigricans* subsp. *nigricans* we have seen, it displays considerable phenotypic variation. The diverse habitats and the inland extension of this taxon may be related to its phenotypic variability. *Vicia nigricans* subsp. *gigantea* manifests fewer phenotypic extremes and is more restricted in habitat.

SELECTED SPECIMENS: Argentina: Chubut —A. A. Beetle & D. Bignoli 224 (US);

FIGURE 6. Illustration of *Vicia nigricans* Hooker & Arnott subsp. *gigantea* (Hooker) Lassetter & Gunn.

Neuquen—A. Burkart 1293 (BAFC), R. Leal & V. Roig 18.212 (BAFC), J. Vallerini 220 (BAFC), T. M. Pedersen 1517 (US); Rio Negro—O. Boelcke & M. N. Correa 5855 (BAFC), L. R. Parodi 11540 (GH), H. A. Senn 4274 (US), F. W. Hunnewell 16,033 (GH). Chile: Colchaqua—G. Montero O. 49A (GH); Concepción—C. Junge K. 16.248 (US); Curico—Bro. Claude-Joseph 5637 (US); Cautin—E. Barros 7601 (BAFC); Malleco—H. Gunckel 16.046 (BAFC); Nueben—F. Philippi & A. Borchers (F); O'Higgins—C. Jiles 4646 (BAFC); Santiago—G. Montero O. 49 (GH); Valdivia—O. Buchtien (GH, US); Valparaiso—J. L. Morisson & R. Wagenknecht 17155 (GH), W. J. Eyerdam 10084 (F, US).

Vicia nigricans Hooker & Arnott subsp. *gigantea* (Hooker) Lassetter & Gunn comb. nov.

Figure 6

Vicia gigantea Hooker, Fl. Bor. Am. 1:157. 1831.

HOLOTYPE: In open wood, common Northwest America, *Douglas* (K!). *V. sitchensis* Bong., Mem. Acad. Sci. St. Peters., ser. 6, 129–130. 1833. *V. hookeriana* Walpers, Rep. Bot. Sys. 1:715–716. 1842. *Lathyrus cinctus* S. Wats. Proc. Amer. Acad. Arts Sci. 23:263. 1888. *Vicia semicincta* Greene Erythea 3:17. 1895.

DESCRIPTION: Coarse, strongly climbing, perennial herb, 6 to 20 dm tall; pubescent when young, becoming less so at maturity, turning black with age or on drying, rarely remaining green; stems stout, 3 to 7 mm thick, fistulose, conspicuously ridged; stipules large (up to 25 mm long and 15 mm wide), upper portion almost foliaceous, lower portion smaller, lacerate–dentate; leaves 9 to 23 cm long ending in a ramose tendril; leaflets alternate or subopposite, 16 to 29, entire, narrowly lanceolate to ovate or elliptic to oblong or oblong–lanceolate, 20 to 50 mm long, 5 to 17 mm wide, rounded, obtuse, or truncate at the mucronulate apex, pubescent when young, mature leaflets somewhat strigose with age and obscurely pellucid dotted below, glabrous with prominently pellucid dots above; flowering peduncles averaging about same length as subtending leaves but shorter or longer, lengthening during fruiting with 6 to 19 closely packed racemose flowers; pedicels 2 to 3 mm long; corolla 10 to 15 mm long, ochreoleucous to orange, often tinged with rose-purple; calyx gibbous, tube one-half length of corolla, upper pair of teeth 0.5 to 1.2 mm long, lateral pair 1.3 to 3.2 mm long, lowest tooth 5.4 to 8.7 mm long and subequal to the tube; androecial sheath oblique at the apex; pollen tricolporate, prolate, 46 × 32 micra; style dorsally flattened, upper portion encircled by delicate hairs; legume glabrous, oblong, 33 to 55 mm long, 10 to 20 mm wide, becoming black at maturity, smooth within, four to eight ovuled, on a 4-mm stipe; seed usually three to four per legume, spherical, smooth, ochre to reddish-ochre, moderately to densely mottled and pointed with darker brown, occasionally with markings so dense as to make seeds appear monochrome dark-brown or purplish-black to velvety black, 5 to 6 mm in diameter, containing canavanine; hilum color of seed coat, circumlinear, occupying 75 percent of the seed circumference.

FLOWERING: May through July. Chromosome number: $n = 7$, Graham Island between Skidegate and Skidegate Village. The voucher (in DAO) is Calder, Savile, and Taylor 34665 (Taylor and Mulligan 1968). $2n = 14$ (S. Veerasethakul, unpublished data).

DISCUSSION: *Vicia nigricans* subsp. *gigantea*, the largest North American vetch, is restricted to the coast of Pacific North America from the environs of Sitka, Alaska, to San Luis Obispo County, California (Figure 4). [Anderson (1959) and Welsh (1974) stated that it is reported from Cook Inlet, which is much further north. This is based on a herbarium specimen collected by W. H. Osgood in 1900 (US). The location on the specimen is incorrect; it was actually collected in the Queen Charlotte Islands (Calder and Taylor 1968 and personal communication).] In the northern portion of its range, *V. nigricans* subsp. *gigantea* usually is

found along the upper margin of sand or shingle beaches in the driftwood zone, on rocky headlands, and in open woods near the coast (Calder and Taylor 1968). In the southern portion of its range, it is found along the coast in moist, usually wooded or shaded places. The only inland incursion is along the Columbia River to the Willamette Valley, Oregon.

SELECTED SPECIMENS: Canada: British Columbia—J. Macoun (US), W. Spreadborough 70.434 (NY), C. F. Newcombe 19 (F), W. H. Osgood (US), J. Macoun 79.704 (NY). United States: Alaska—M. W. Gorman 55 (NY, US), Mr. & Mrs. E. P. Walker 989 (F, NY, US), J. P. Anderson 833 (NY); California—Alameda County, V. K. Chesnut (US); Contra Costa County, W. C. Blasdale (US); Humboldt County, C. R. Gunn 2691 (US); Mendocino County, J. McMurphy 157 (NY, US); San Mateo County, C. F. Baker 506 (NY, US); Santa Cruz County, C. R. Gunn 2654 (US); Oregon—J. T. Howell (F, NY, US); Multnomah County, E. P. Sheldon, S. 12033 (F); Washington County, A. Kellogg & W. G. W. Harford 174 (US); Washington—Clallam County, C. R. Gunn & C. E. Smith, Jr., 3670 (NA, US); Jefferson County, C. R. Gunn & C. E. Smith, Jr., 3671 (US); Pacific County, W. W. Eggelston 11478 (F, US); Whatcom County, W. N. Suksdorf 964 (F, NY, US).

DISCUSSION OF DISTRIBUTION

A distribution pattern similar to that of *Vicia menziesii* and *V. nigricans* subsp. *nigricans* and subsp. *gigantea* is exhibited by *Fragaria chiloensis* (Linnaeus) Duchesne (Darrow 1966). In fact, the distribution is almost identical with disjunct varietal populations of *F. chiloensis* in coastal and mountain areas of Chile and western Argentina, along the Pacific coast from California to the Aleutian Islands, and above 1800 m in the mountains of Hawaii. No explanation of the *Fragaria* distribution was offered by Darrow.

Although there are several possible explanations for the distribution of the *Vicia* taxa, two appear to be more likely than the others. Ancestral *V. menziesii* may have been transported from the Pacific Northwest to Hawaii by ocean currents or by migratory birds. Although ocean currents may transport buoyant, viable seeds and seed-bearing fruits over thousands of kilometers, there is no direct transport current from the Pacific Northwest to Hawaii (Gunn, Dennis, and Paradine 1976). In an analysis of the Hawaiian flora, Carlquist (1974) found examples of 52 successful arrivals from American sources. He concluded that repetitive in-seawater drifting was unlikely from the Americas. Rare or infrequent rafting by logs also was unlikely, though six logs bearing Pacific Northwest brands have been stranded on Hawaiian beaches (Strong and Skolmen 1963). Unfortunately, the authors neither related these strandings to ocean currents, storms, or tsunamis, nor to where these logs entered the Pacific Ocean.

Carlquist (1974) believes, as do many others, that dispersal of seeds and small fruits by migratory birds is probably the method by which most groups of angiosperms arrived on the high islands of the Pacific. The presence of *Vicia menziesii* on Hawaii Island is best explained, Carlquist said, by internal transport by birds, and we agree.

Raven (1963) compiled information concerning temperate North and South American disjuncts. Although *Vicia nigricans* subsp. *gigantea* and *V. nigricans* subsp. *nigricans* were not included, they are an additional example similar to those he did include. Raven believes that long-distance bird dispersal is the most logical explanation of most of the disjuncts. Another possibility would be migration over a land bridge or continuous mountain chains that would have allowed direct movement through the tropics to the temperate zones. He believes this method less supportable, because of a lack of corresponding animal disjuncts that would be expected were a continuous route available. Lincoln (1935) stated that the Pacific Flyway is the longest migration route in the Americas and that a number of species migrate from Alaska to southern South America along this route. Lincoln (1952) and Dorst (1962) also cite several species of migrating birds

that travel from Alaska to Hawaii and beyond.

Cruden (1966) believes that long-distance migration dispersal may not be as attractive an explanation as previously believed. A major point he makes is that internally transported seeds (these are more likely to be successfully carried great distances as opposed to those carried externally) do not remain in the digestive tract long enough. However, Proctor (1968) and Vlaming and Proctor (1968) present data that demonstrate that shore birds can retain seeds long enough to transport them the required distances, even to the most remote oceanic islands. They found that larger seeds (2–6 mm in diameter) with a hard impervious seed coat were best retained, and that some shore bird species tend to retain seeds better than other species they studied. Seeds of the *Vicia* spp. in this study are 5 to 8 mm in diameter and are hard-seeded.

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LITERATURE CITED

ANDERSON, J. P. 1959. Flora of Alaska and adjacent parts of Canada. Iowa State University Press, Ames.

ANDREWS, K. S., and J. B. PRIDHAM. 1967. Melanins from dopa-containing plants. Phytochemistry 6:13–18.

BALL, P. W. 1968. *Vicia*. Pages 129–136 *in* T. G. Tutin, et al., eds. Flora Europaea. Vol. 2. Cambridge University Press, Cambridge.

BELL, E. A. 1966. Amino acids and related compounds. Pages 195–209 *in* T. Swain, ed. Comparative Phytochemistry. Academic Press, New York.

———. 1971. Comparative biochemistry of non-protein amino acids. Pages 179–206 *in* J. B. Harborne, D. Boulter, and B. L. Turner, eds. Chemotaxonomy of the Leguminosae. Academic Press, New York.

BELL, E. A., and A. S. L. TIRIMANNA. 1965. Associations of amino acids and related compounds in the seeds of forty-seven species of *Vicia*: Their taxonomic and nutritional significance. Biochem. J. 97: 104–111.

BURKART, A. 1966. Las leguminosas sylvestres y cultivadas. Acme Agency, Buenos Aires.

CALDER, J. A., and R. L. TAYLOR. 1968. Flora of the Queen Charlotte Islands. Part 1. Queen's Printer, Ottawa.

CARLQUIST, S. 1974. Island biology. Columbia University Press, New York.

ČINČURA, F. 1962. Poznákmy k cytológii druhov rodu *Vicia* L. zo slovenských

nálezísk II. Acta Fac. Rerum Nat. Univ. Comenianae Bot. 7:349–388.

———. 1973. Angaben über die Zahl und die Morphologie der Chromosomen von *Vicia dumetorum* L. und deren Vergleich mit *Vicia pisiformis* L. Acta Fac. Rerum Nat. Univ. Comenianae Bot. 21:103–107.

CLARKE, G. C. S., and F. K. KUPICHA. 1976. The relationship of the genus *Cicer* L. (Leguminosae): The evidence from pollen morphology. Bot. J. Linn. Soc. 72:35–44.

CORTAZAR, C. S. DE. 1948. Observaciones chromosomaces en seis especies Chilenas. Agri. Tecn. (Chile) 8:28–36.

CRUDEN, R. W. 1966. Birds as agents of long-distance dispersal for disjunct plant groups of the temperate western hemisphere. Evolution 20:517–532.

DARROW, G. M. 1966. The strawberry. Holt, Rinehart, and Winston, New York.

DEGENER, O., I. DEGENER, and C. R. GUNN. 1970. *Vicia menziesii* Spreng. Unnumbered supplemental page for family 169 *in* O. Degener and I. Degener, eds. New illustrated flora of the Hawaiian Islands. Published by the authors, Volcano, Hawaii.

DORST, J. 1962. The migrations of birds. Houghton Mifflin, Boston.

ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Chronica Botanica, Waltham, Mass.

FEDTSCHENKO, B. A. 1948. *Vicia*. Pages 406–475 *in* V. L. Komarov, Flora U.S.S.R. Vol. 13. Akad. Nauk S.S.S.R., Moscow.

FOSBERG, F. R., and D. HERBST. 1975. Rare and endangered species of Hawaiian vascular plants. Allertonia 1:1–72.

GUNN, C. R. 1968. The *Vicia americana* complex (Leguminosae). Iowa State J. Sci. 42:171–214.

———. 1970. A key and diagrams for the seeds of one hundred species of *Vicia* (Leguminosae). Proc. Internat. Seed Test. Assoc. 35:773–790.

———. 1971. Seeds of native and naturalized vetches of North America. U.S. Dept. Agr. Agr. Handb. 392. U.S. Govt. Printing Office, Washington, D.C.

GUNN, C. R., and J. KLUVE. 1976. Androecium and pistil characters for tribe *Vicieae* (Fabaceae). Taxon 25:563–575.

GUNN, C. R., J. V. DENNIS, and P. J. PARADINE. 1976. World guide to tropical drift seeds and fruits. Quadrangle/New York Times, New York.

HEITZ, E. 1931. Nukleolen und Chromosomen in der Gattung *Vicia* L. Planta 15: 495–505.

HERMANN, F. J. 1960. Vetches of the United States—native, naturalized and cultivated. U.S. Dept. Agr. Agr. Handb. 168. U.S. Govt. Printing Office, Washington, D.C.

HILLEBRAND, W. 1888. Flora of the Hawaiian Islands. Williams and Norgate, London.

HOLMGREN, P., and W. KEUKEN. 1974. Index herbariorum. Part 1. The herbaria of the world. 6th ed. Regnum Veg. 92:1–397.

KUPICHA, F. K. 1976. The infrageneric structure of *Vicia*. Notes Roy. Bot. Gard. Edinburgh 34:287–326.

———. 1977. The delimitation of the tribe Vicieae (Leguminosae) and the relationships of *Cicer* L. Bot. J. Linn. Soc. 74: 131–162.

LASSETTER, J. S. 1972. A biosystematic study of the *Vicia ludoviciana* complex (Leguminosae). Microfilm 73-9458. University Microfilms, Ann Arbor, Mich.

———. 1975. Taxonomic status of *Vicia hassei* (Leguminosae). Madrono 23:73–78.

———. 1978. Seeds of some native American vetches. Sida Contrib. Bot. 7:255–263.

LINCOLN, F. C. 1935. Ancestral highways of the sky. Amer. Forests 41:157–159, 196.

———. 1952. Migration of birds. Doubleday, New York.

MANN, H. 1866. Enumeration of Hawaiian plants. Proc. Amer. Acad. Arts Sci. 7:143–235.

METTIN, D., and P. HANELT. 1968. Bemerken zur Karyologie und Systematik einiger Sipper der Gattung *Vicia* L. Feddes Repert. Z. Bot. Taxon. Geobot. 77:11–30.

MOORE, D. M., and B. SCOTTER, 1976. *Vicia* L. in Tierra del Fuego. Darwiniana 20: 371–386.

NOZZOLILLO, C. N. 1977. Identification of *Vicia* seedlings. Can. J. Bot. 55:2439–2462.

PROCTOR, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160:321–322.

RAVEN, P. H. 1963. Amphitropical relation-

ships in the floras of North and South America. Quart. Rev. Biol. 38:151–177.

REICHE, C. 1898. Flora de Chile. Volume II. Imprenta Cervantes, Santiago.

ROCK, J. F. C. 1920. The leguminous plants of Hawaii. Unnumbered publication by Exp. St. Hawaii Sugar Plant. Assoc., Honolulu.

SHRIVASTAVA, L. M. 1963. Cytogenetical studies in certain species of *Vicia*. Cytologia 28:154–169.

SKOTTSBERG, C. 1931. Remarks on the flora of the high Hawaiian volcanoes. Acta Horti Gotob. 6:47–65.

STANKEVICH, A. K. 1970. On clarification of the *Vicia* L. genus systematics. Tr. Prikl. Bot. Genet. Sel. 43:110–125.

STRONG, C. C., and R. G. SKOLMEN. 1963. Origin of drift-logs on the beaches of Hawaii. Nature 197:890.

SVESHNIKOVA, I. N. 1927. Karyological studies in certain species of *Vicia*. Tr. Prikl. Bot. Genet. Sel. 17:37–72.

TAYLOR, R. L., and G. A. MULLIGAN. 1968. Flora of the Queen Charlotte Islands. Part 2. Queen's Printer, Ottawa.

TERZIISKI, D. P. 1974. Cytotaxonomic studies on Bulgarian leguminous species: The karyotype of *Vicia dumetorum* L. C. R. Acad. Bulg. Sci. 27:1267–1270.

TSCHIERSCH, V. B., and P. HANELT. 1967. Die freien Aminosäuren der Samen von *Vicia* L. und die Systematische Gliederung der Gattung. Flora (Jena) Abt. A. Physiol. Biochem. 157:389–406.

UNITED STATES DEPARTMENT OF THE INTERIOR. 1978. Determination that various plant taxa are endangered or threatened species. Federal Register 43(81):17910–17916.

VLAMING, V. L. DE, and V. W. PROCTOR. 1968. Dispersal of aquatic organisms: Viability of seeds recovered from the droppings of captive killdeer and mallard ducks. Amer. J. Bot. 55:20–26.

WELSH, S. L. 1974. Flora of Alaska. Brigham Young University Press, Provo.